Net gains: Seabird movement reveals the ecological footprint of fishing vessels

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Exploitation of the seas is currently unsustainable, with increasing demand for marine-derived resources placing intense pressure on the Earth's largest ecosystem [1]. The scale of anthropogenic effects varies from local to entire ocean basins [1,2,3], and effective management requires a thorough understanding of the mechanisms underpinning these drivers of change. For example, the production of discards by commercial capture fisheries is a multi-scale phenomenon that can have both positive and negative impacts on scavengers at the population and community-level [2,3,4,5,6], although this is driven by individual foraging behaviour [3,7]. Currently, we have little understanding of the scale(s) at which individual animals initiate such behaviours, which is problematic because this is critical in assessing current effects and predicting future impacts of global change. We use the known interaction between fisheries and a wide-ranging seabird, the Northern gannet *Morus bassanus* (hereafter gannet) [3], to investigate how fishing vessels affect individual birds' behaviours in near real-time. We document the footprint of fishing vessels' (≥15 m length) influence on foraging decisions (≤11 km), and a potential underlying behavioural mechanism, by revealing how birds respond differently to vessels depending on gear type and activity. Such influences have important implications for fisheries (including the proposed discard ban [8]) and wider marine management such as the implementation of marine protected areas.

Fish and fisheries management are major environmental and political issues [1,4,8]. Understanding the spatial influence of fisheries is critical to marine planning and policy, including shipping, offshore development, bycatch and fisheries themselves [1,4,8], but its true ecological footprint is currently unknown. The issue of scale is particularly important to the ecology and conservation of a suite of wide ranging marine predators, where studies of scale-dependent foraging strategies [2,3,5] have yet to resolve mechanisms used to locate patchy prey, and where spatial planning lacks a landscape scale. To address this knowledge gap we analysed high resolution GPS tracking data from 74 chick-rearing gannets contemporaneously tracked from six breeding colonies during Jun-Jul 2011 (Table S1); and combined this with anonymised fisheries data from the Vessel Monitoring System (VMS) within the Irish Exclusive Economic Zone (EEZ). We are thus able to characterize the impact of fishing vessels on seabird behavior at a range of colony sizes with varying competitive and environmental gradients [3,7], and throughout a national management unit [8]. Using an ethoinformatics approach based on flight speed and tortuosity, gannet GPS locations were assigned one of two behavioural states: ‘foraging’ or ‘commuting’ [7; Supplemental Information). The distance to nearest vessel, vessel type (comprising trawlers and non-trawlers due to differences in discard opportunities; Supplemental Information) and vessel activity (‘drifting’, ‘fishing’ or ‘steaming’, based on instantaneous vessel speed and gear-specific fishing speeds; Supplemental Information) were appended to every gannet location. We used multi-state Markov models to examine the influence of vessel distance, type and activity on the transition probabilities between the behavioural states of individual birds during foraging trips (for full details see Supplemental Information).

Our models reveal that gannet behavior is influenced by fishing vessels at distances up to 11 km, with significant deviation from the null transition probability between states first detected at this range (Fig 1 a) (after controlling for significant effects of both sex and colony; Fig S1, Supplemental Information). This is the first estimate of the size of the ecological footprint of a fishing vessel, and suggests how individual behavioural decisions can underly broad-scale correlations between fisheries and seabird distributions [2,5].

While the presence of fishing vessels alone has a significant impact on seabird behavioural responses, there is a small possibility that the relationship exists because both humans and birds are exploiting the same productive fishing areas [5]. Thus we further investigated bird-boat interactions based on vessel type and activity, limiting bird locations to those within the 11 km response threshold. Distance to vessel remained an important predictor of behavioral switching with birds becoming increasingly likely to switch to foraging and less likely to switch to commuting with increasing proximity to a vessel (11.1 % per km, 4.7 % per km respectively). More importantly, there was a strong interaction between the effects of vessel type and vessel activity on bird behavioural transition probabilities. Gannets were significantly more likely to switch to foraging, and significantly less likely to switch to commuting behavior when vessels were fishing; and significantly more likely to switch to commuting when trawlers were steaming or drifting (Fig 1 b, c). Effects were different for non-trawlers where discard opportunities differ – birds were more likely to switch to foraging, and less likely to switch to commuting when non-trawlers were drifting compared to fishing, likely reflecting the processing of catch on these vessels (Fig 1 b,c). It thus appears that individual gannets are able to reliably differentiate between both vessel types and vessel activity and adjust their behavior accordingly. Attraction to boats can be enhanced by the presence of con- or hetero-specifics already in attendance [9,10], and may strengthen depending on species and time of year [5,6,10]. Birds may therefore be particularly attuned to identifying specific behaviours or characteristic cues, and are capable of applying these to human fishers, triggering similar behavioural responses [10].

In the marine environment vessels alone can significantly affect the distribution or behavior of many species through disturbance and attraction [1,5,9]. Here we identify the scale at which attraction occurs in a presumed visual forager (gannets have no external nostrils and relatively small olfactory bulbs) and demonstrate a potential behavioural mechanism at the individual level, underlying the broad patterns of association observed between seabirds and fishing vessels [2,3,5]. At a fundamental level the response of individual birds to the presence of humans as top predators [2,9,10] can have important effects on population processes [4,6]. From an applied perspective, understanding these local-scale processes, and the way in which they influence broader patterns across national territorial waters, is vital for effective marine planning and fisheries management, particularly in light of proposed fisheries reform [8]. Our results suggest that each vessel can significantly influence the distribution and foraging patterns of wide-ranging marine predators.

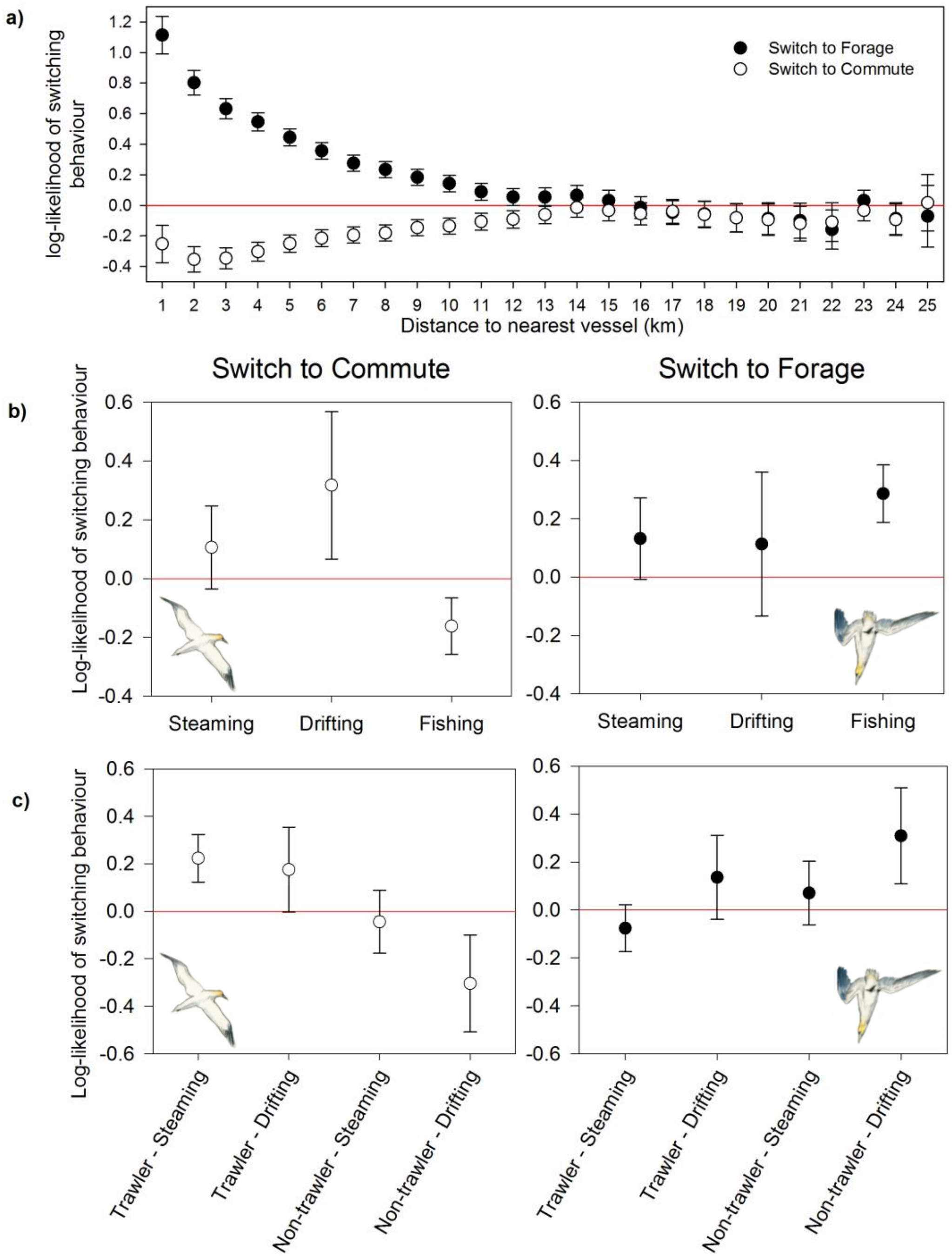

Fig 1. Influence of fishing vessels on seabird behavior. 95% CIs passing through zero (red line) indicate no significant effect on transition probabilities.

a) Influence of vessel proximity on the log-likelihood of gannets switching between behavioural states (commute to forage - filled circles; forage to commute - open circles). At distances ≤11 km, gannets are significantly less likely to switch from foraging to commuting and also significantly more likely to switch to foraging behavior.
b) Effect of closest vessel type across different fishing activities on gannet behavioural transition rates (log-likelihood ± 95% CIs). Values compare between trawlers and non-trawlers for each behavioural switch, with those

passing through zero indicating no significant difference between vessel types. When vessels travel at fishing speeds, gannets are more likely to switch to foraging, and less likely to switch to commuting, when vessels are trawlers as opposed to non-trawlers. Birds are also more likely to switch to commuting when trawlers are drifting.

c) Effect of closest vessel activity within vessel types on gannet behavioural transition rates (log-likelihood ± 95% CIs). Values compare activities to the baseline that each vessel type is fishing for each behavioural switch. Gannets are more likely to switch to commuting when trawlers are steaming compared to fishing. Birds are less likely to switch to commuting, and more likely to switch to foraging, when non-trawlers are drifting compared to fishing. These differences likely reflect contrasting discard availabilities between vessel types.

Supplemental Information
Supplemental Information includes details on experimental procedures, statistical analyses and one figure.

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Supplemental Information

Data Collection

All tracked birds were caught at the nest during changeover while attending 2 – 5 week old chicks (for numbers captured and colony details see Table S1). The bird that had been incubating was captured at the nest using a metal crook or brass noose attached to a carbon-fibre pole and a GPS logger (either i-gotU GT-200, Mobile Action Technology Inc, 37 g or e-obs, GmbH, Munich, 45 g depending on colony accessibility) was attached to the central tail feathers using Tesa© tape. These devices were set to record a position every 2 mins. Birds were captured from seven of the eight colonies known, or with the potential, to forage in Irish territorial waters, with devices successfully retrieved from six of these colonies (Table S1). No devices could be retrieved from one small colony due to persistent bad weather preventing access, and one small colony is inaccessible. However, colonies where birds were successfully tracked comprised > 97 % of all breeding individuals within the geographic area.

Colony	Location	Size (AON)	Device Type	Devices Retrieved
Ailsa Craig	55º 15’ N 05 07’ W	27 100	e-obs GPS	13 (100 %)
Bull Rock	51 35’ N 10 18’ W	3 700	i-gotu 200	14 (50 %)
Grassholm	51 44’ N 05 29’ W	39 000	i-gotu 200	17 (65 %)
Great Saltee	52 07’ N 06 37’ W	2 400	i-gotu 200	18 (60 %)
Lambay	53 30’ N 06 00’ W	200	i-gotu 200	3 (43 %)
Little Skellig	51 47’ N 10 30’ W	29 700	e-obs GPS	9 (90 %)

Table S1: Details of study colonies and tracking devices retrieved. AON - apparently occupied nests. Percentages displayed in brackets indicate proportion of deployed devices where data was successfully retrieved from known sex birds.

A small blood sample (< 1 ml) was taken under license from the tarsal vein of all birds on capture. Samples were kept cool before being spun in a centrifuge at 13 000 rpm for five mins within six hrs of sampling. Following separation of red blood cells and serum, samples were stored on ice. DNA was extracted from 2 µl of red blood cells using an ammonium acetate protocol [S1], and individuals were sexed using the 2757R [S2] and 2550F [S3] primers. Sexing revealed 36 male and 38 female gannets within our tracked individuals.

All fishing vessels ≥ 15 m in length are required under EU law to provide a GPS position at least every 2 hrs together with information on speed [S4]. These vessels are also obliged to record the gear type(s) used on a daily basis [S5, S6]. Due to issues surrounding confidentiality of individual fishers [S7], vessel monitoring system (VMS) data were anonymised, and only datapoints relevant to our analyses of gannet locations were released for analysis. The nearest vessel location up to a maximum of 30 km based on theoretical maximum visibility limits [S8] was assigned to each individual bird location. If no vessels were within 30 km of a fix, it was not included in the analysis (4764 datapoints, < 0.05% of datapoints). As the time interval between recorded VMS positions differs from the time interval of the gannet GPS positions, vessel positions were inferred for each of the gannet positions using straight-line interpolation between consecutive VMS fixes.

Discrimination of behavior from locations

Gannets forage almost exclusively during daylight hours, with birds resting on the sea surface at night [S9]. The principle method of prey capture is plunge-diving, typically following a searching pattern involving a reduction in speed and increase in tortuosity [S9, S10]. Location points were therefore omitted from all analyses if they occurred at night, or were less than 5 km from the colony (observation from colonies (T Bodey, M Jessopp pers obs) and examination of GPS tracks revealed no foraging behaviour within these buffers). Locations outside of the Irish EEZ were also excluded as we unable to obtain equivalent resolution of VMS data from UK waters [S7]. The temporal resolution of GPS data was standardised to 2 mins and all incomplete trips were removed from the analysis. This resulted in a total of 530 foraging tracks (range per individual 1-21) over the monitoring period, comprising > 150,000 data points.

Points were assigned as 'foraging' based on measured speed and tortuosity, and were considered to be putative foraging locations if any of the following criteria were met: a) tortuosity < 0.9 and speed > 1 m/s; b) speed > 1.5 and < 9 m/s; c) tortuosity > 0.9 and acceleration < -4 m/s^2, based on previous foraging studies of gannets [S11]. Points typical of resting on the surface for brief periods were included within foraging as this behaviour typically occurs following both successful and unsuccessful prey capture [S12]. Indeed, 91% of all transitions involving a rest state were from or to foraging in our dataset. All other points were considered to be 'commuting' behaviour.

Vessel activity can be characterized from VMS data depending on gear-specific travelling speeds (Table S2) as a) drifting – vessel below minimum fishing speed, so waiting for the tide, mending or hauling gear etc ; b) fishing – vessel between minimum and maximum fishing speeds for its gear type; c) steaming – vessel exceeding maximum fishing speed for its gear type. [S6]. Vessels locations missing information on either gear type or speed were omitted (< 3 % of all vessel locations). While vessels were not individually monitored during this study, previous research demonstrates that instantaneous vessel speed gives a high level of vessel behavior classification accuracy, with fishing operations particularly well identified [S6]. For every gannet location, the distance to nearest vessel, the fishing gear carried ('vessel type') and instantaneous speed ('vessel activity') were appended.

Gear Type	Minimum fishing speed (knots)	Maximum fishing speed (knots)
Pots	0.1	4.5
Gillnets	0.1	4.5
Bottomtrawls	0.5	5.5
Dredges	0.5	5.5
Seines	0.5	4.5
Pelagic Trawls	0.5	6
Longlines	0.1	4.5

Table S2: Gear-specific minimum and maximum fishing speeds based on examination of vessel speed profiles for vessels equipped with a Vessel Monitoring System operating in Irish waters.

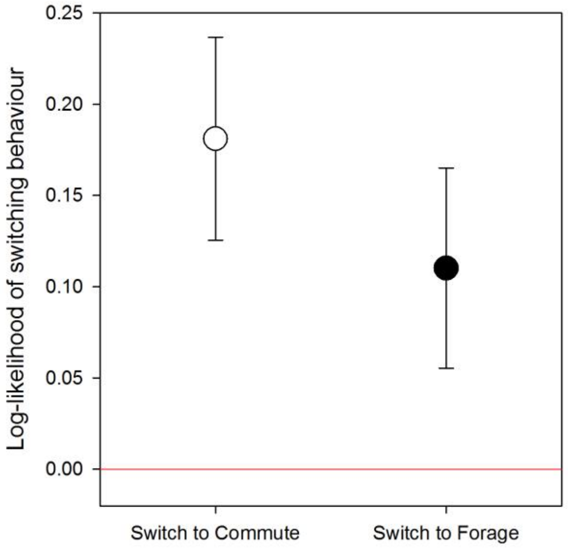
Multi-state Models

All multi-state models were implemented in the msm package in R version 2.15.2 [S13, S14]. These models describe how an individual moves between discrete states in a continuous time series, where the future state depends on the current state [S13]. The use of fixes every 2 mins ensures that sampling times can be disregarded as they are fixed in advance. All relative model performance comparisons were assessed through likelihood ratio tests.

An initial model was used to determine the impact of vessels at increasing distance from gannet locations. Given their known potential impact on bird behaviour, the sex and colony of origin of birds were included. For example, it is known that at one of our study colonies (Grassholm), male gannets incorporate a greater proportion of fisheries discards in their diet [S15], and also exhibited an increased proportion of searching behaviour in association with fishing vessels [S16]. Colony of origin is also likely to partly determine access to discards as birds from different colonies exhibit strong spatial partitioning in foraging location [S11], and discards are not evenly distributed throughout the Irish EEZ [S17]. Distance to nearest fishing vessel was binned in 1 km increments, and incorporated as a binomial variable (i.e. recorded as 1 if a bird location is within *i* km of a vessel location, 0 otherwise). This method was used to determine at what distance from vessel locations transition rates between bird behavioural states differed significantly from random. Step-wise decreases in distance between vessel and bird locations were run, starting at 25 km to ensure inclusion of the estimated visual distance to the horizon for seabirds flying at average heights above sea level (15 km, S8).

Once detection distances that produced significant effects on transitional probabilities had been established, a second model was used to examine the impact of vessel type and activity within this range. The total dataset was thus reduced to only those bird locations within 11 km of a fishing vessel, and this reduced dataset contained > 105,000 locations, while still incorporating all individuals. Bird sex and colony of origin were included as blocking factors given their demonstrated impact in the initial analysis above, and distance to vessel was included as a continuous variable. While gannets may associate with smaller fishing vessels, evidence from bird-borne cameras revealed only large fishing vessels (> 15 m), and no interactions with artisanal boats [S16]. In addition, the type and quantity of discards differs significantly between trawlers and other gear types, with the majority of discards resulting from trawl fisheries [S18]. Given this empirical evidence, vessel types were classified as trawl (bottom or pelagic trawl) or non-trawl (all others), with vessel behaviour classified according to gear-specific fishing speeds prior to merging by vessel type.

a)



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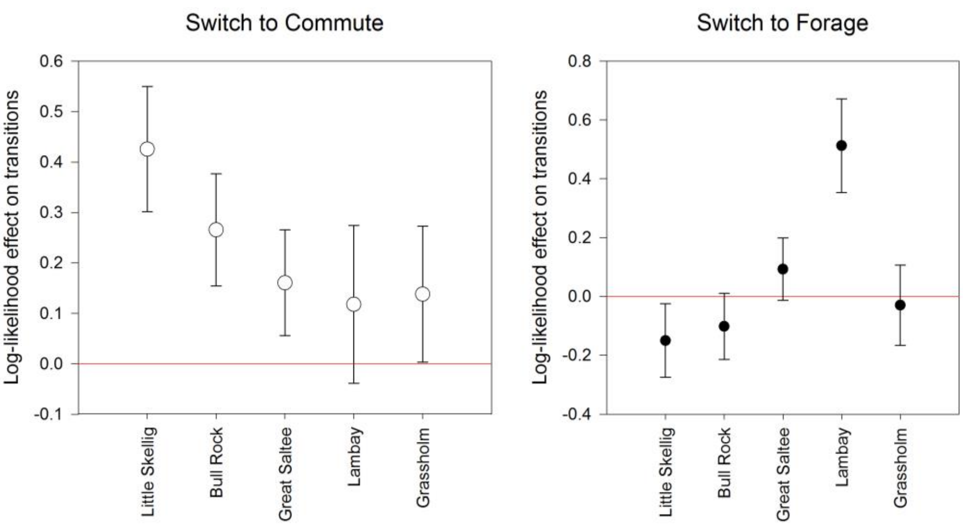

Fig S1. Effect of sex and colony on transitions between gannet behavioural states log-likelihood of effects ±95 % CIs). 95% CIs passing through zero (red line) indicate the effect is non-significant.
a) Effect of sex. Values compare between the sexes for each behavioural switch, with those passing through zero indicating no significant difference between the sexes. Male gannets are significantly more likely to switch both from commuting to foraging and from foraging to commuting, suggesting more variable behavior in males compared to females, potentially reflecting male gannets' increased exploitation of short-lived foraging opportunities at fishing vessels.
b) Effect of colony. Colonies are aligned from west to east, with baseline comparison to the most easterly colony (Ailsa Craig). More westerly colonies are more likely to switch to commuting behavior, with the most westerly colony also less likely to switch from commuting to foraging. This suggests a geographical impact on transition rates

likely reflecting different environmental conditions such as tidal fronts around the Irish landmass.

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